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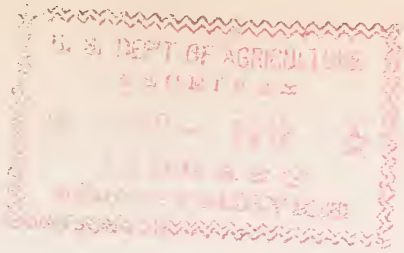

Issued October 4, 1912.

U. S. DEPARTMENT OF AGRICULTURE,

BUREAU OF ENTOMOLOGY—CIRCULAR No. 161.

L. O. HOWARD, Entomologist and Chief of Bureau.

THE MANIPULATION OF THE WAX SCALES OF THE HONEY BEE.

BY

D. B. CASTEEL, Ph. D.,

Collaborator; Adjunct Professor of Zoology, University of Texas.

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INTRODUCTION.

The particular form of bee activity with which this paper deals is that which results in the removal of the wax scales from the bodies of the worker bees and in the application to the comb of the wax thus obtained. A detailed presentation of the facts will be given and attention called to certain current conceptions of this process which are in error.

Since the bee is a very lively insect it is not surprising that the bodily movements upon which some of its activities depend are extremely difficult to follow and may easily be misunderstood. All of its highly specialized legs may be used at once in the performance of some intricate process, and the observer is in need of keenness of sight and patience if he would gain more than an approximate understanding of the parts taken by the several members.

In the more permanent literature of apiculture and of zoology will be found well-written accounts of the habits of bees, accounts which are founded upon a large amount of careful observation and which represent the work of many students of bees from the time of Huber on. As the years have gone by, errors of sight and of judgment have gradually been eliminated, so that at the present time our knowledge of bee life, so far as it goes, rests upon a fairly satisfactory foundation of authenticated facts. Yet many puzzling questions are still unanswered, and some supposed facts may still be doubted.

An examination of a number of bees from an active colony will show great variation in the appearance of the wax scales of differ-

ent members of the colony. In some cases no scales can be observed, even upon dissection. In others the scales will be found to be extremely thick and completely filling the wax pockets. Some bees will show scales in two or three pockets and none in others. Many of the workers will possess a complete supply of scales, either all of about the same thickness or varying considerably in thickness. These and other diverse conditions present themselves for explanation.

The present account is particularly concerned with the manipulation of the wax scales. By what process or series of processes are the scales of wax removed from their pockets and added to the comb? That the wax which forms the comb is produced by the bees themselves, being elaborated within their bodies and given out in the form of thin plates or scales, is a fact well known to all students of bees; but many differences of opinion have been expressed concerning the exact method of wax manipulation. It is also well known that the workers of the hive perform many duties—building the comb, gathering the stores of pollen and honey, caring for the brood and the queen, repairing, cleaning, ventilating, and guarding the hive—and it has been fairly well established that in some cases, at least, these duties vary with the age of the individual worker, although more accurate information on this point is much to be desired. Dreyling's[1] results, in particular, indicate that bees of certain ages are incapable of producing wax, since their glands are either undeveloped or atrophied. Do these bees use the wax secreted by others, taking it from them, manipulating it, and forming it into comb? By careful observation bees devoid of wax scales or with scales too thin for satisfactory removal may be discovered working with the wax. Do these bees procure their wax from other workers, or are they merely reworking the wax of the comb? Upon each hind leg of a worker bee is located a peculiar pincers-like structure long known as the wax shears. Do bees really use this instrument in extracting the scales from the pockets, and if so, does the owner of the scale perform this operation, or is the scale removed by another worker? Or may it not be that the wax scales drop from their pockets when they reach a suitable thickness, and are salvaged by other workers and added to the comb? All of the above interpretations of these processes have been advanced by various observers. It is the object of this paper to present a true account of the manner in which the scales of wax are transported from their pockets to the comb and to point out some of the causes which lead to diversity in scale number and scale form.

[1] Dreyling, L. 1903. Ueber die wachbereitenden Organe der Honigbiene. Zoologischer Anzeiger, Vol. 26.

Same.—1905. Die wachbereitenden Organe bei den gesellig lebenden Bienen. Zoologische Jahrbücher, Abtheilung für Anatomie u. Ontogenie d. Thiere, Vol. 22.

THE WAX-PRODUCING ORGANS.

The way in which the wax scales are formed, as secretion products arising from the surfaces of the wax plates on the ventral side of the abdomen of the workers, has been well described by others and with apparent accuracy. The accounts of Dreyling embody the results of a very considerable amount of work, and will, for the present, at least, be taken at their full value. The work of Snodgrass[1] upon the anatomy of the wax plates and wax glands may be relied upon. Only a brief statement will here be given of the structure of these organs and of the manner in which the scales are formed.

As is well known, wax is produced by the worker bees only. The location of the wax-secreting surfaces, or wax plates, may be readily determined by an examination of the ventral surface of a bee's abdomen. By stretching the abdomen somewhat it will be seen that each of the last four visible sternal or ventral plates is divided into two regions: A posterior projecting edge which is distinctly hairy, and a smooth anterior half which is usually covered by the next preceding plate. This anterior region is divided by a median ridge into two distinct, irregularly oval areas, which thus lie on either side of the midventral line. These areas are the wax plates, and upon them the wax scales are formed. Each one of the last four sternal plates bears two wax plates, making eight in all. (See fig. 1.)

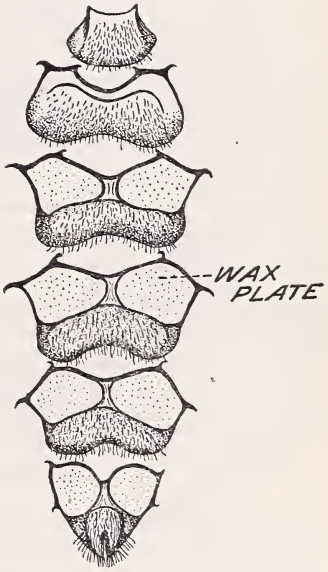

FIG. 1.—Ventral abdominal plates of a worker bee dissected to show the position of the wax plates. (Original.)

The glands which secrete the wax lie on the floor of the abdomen immediately above and in contact with the wax plates, and their secretion is deposited upon the external surfaces of the plates, exuding through the many minute pores which perforate the plates. Upon coming in contact with the air the fluid wax hardens, forming a covering over the entire outer surface of the plate, which gradually increases in thickness with the continued addition of wax through the pores. In this way the wax scales are produced, and since they are

[1] Snodgrass, R. E., 1910. The Anatomy of the Honey Bee, Bur. Ent., Tech. Ser. 18, U. S. Dept. Agr.

molded upon the surfaces of the eight wax plates they correspond to them in number and in form.

In its natural position each wax scale lies between its wax plate and the overlapping edge of the next preceding sternal plate. The scale thus fits into a little crevice or wax pocket and is well protected from injury. If the bee extends its abdomen the rear edges of the scales can be seen protruding from their pockets, or if the scales become very thick they will push the covering sternal plates outward and will project from the pockets.

THE FORMATION OF THE WAX SCALES.

The problem of wax secretion has been extensively studied by Dreyling, who shows that the wax glands differ markedly in structure in bees of different ages. In the newly emerged bee the epidermis which underlies the wax plate is composed of epithelial cells nearly cubical in form. As the bee grows older these cells become elongated and are separated by clear spaces, and when the bee has reached the height of its activity as a wax producer these gland cells are elongated and show liquid wax stored in the spaces between them. When the wax-secreting period is over these cells degenerate, so that in sections through the glands of old field bees, or of bees that have lived over winter, the layer of cells beneath the wax plates appears greatly shrunken, and individual cells can be distinguished by their nuclei only. These histological data are given by Dreyling in support of the conclusion that the secretion of wax in much more abundant at a certain period in the bee's life and that old bees and very young bees are, as a rule, incapable of wax production. These conclusions are in harmony with the practical experiences of bee keepers.

METHODS OF OBSERVATION.

In a study of the behavior during scale removal and wax building it is necessary to watch the bees while they are working naturally within the hive. To accomplish this, observatory hives are used in which glass is substituted for wood in part of the construction. Most of the work is done upon colonies in modified nucleus boxes (fig. 2). The two sides are removed from each hive and are replaced with glass in the form of sliding doors, two to a side, and glass plates are fitted to the top. In all cases wooden shades cover both sides and top when the bees are not under observation. Although bees are somewhat disturbed when light is first admitted to the hive, they appear to become accustomed to it and work normally unless the hive is left open for too long a period.

When a hive is well crowded with bees, and when the frames are widely spaced, the workers are apt to extend the comb above the level of the top bars of the frames until it comes in contact with the glass. This gives the observer an excellent opportunity to study the comb

workers at close range, and it also obviates the necessity of placing glass ends in the hive against which comb might be built.

Even with the best of arrangements it is difficult to follow some of the movements of the workers during the act of scale removal. As an aid to vision a Zeiss binocular microscope is used, the tubes being removed from the stand and held to the eye after the manner of a field glass. By the use of this instrument a bee appears to acquire

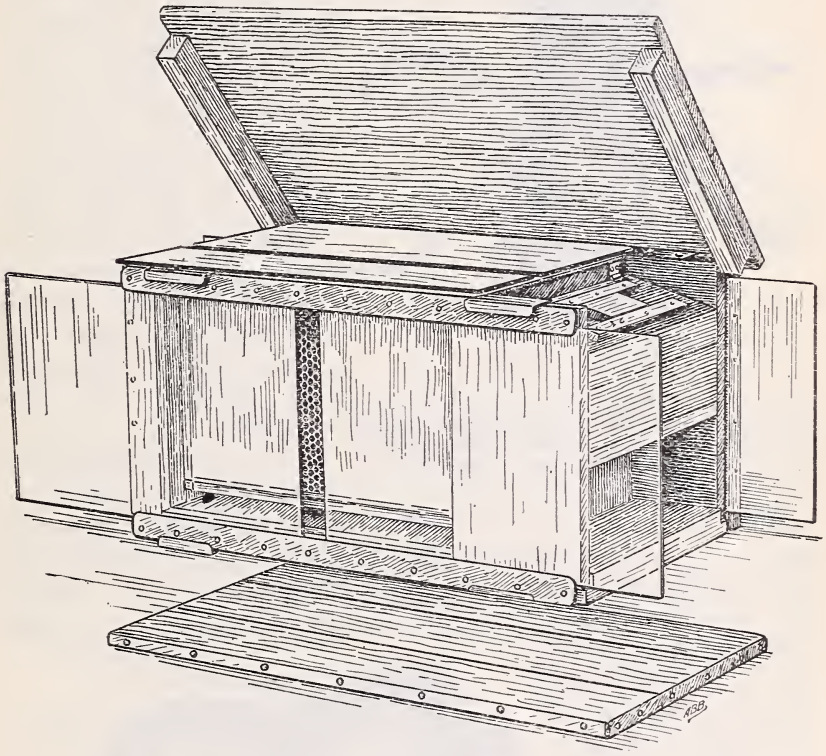

FIG. 2.—Observatory hive. The sides are fitted with sliding glass doors, and two pieces of glass cover the top. The sliding glass doors allow the observer to gain access to any small area of the outer comb without removing the glass from the entire side of the hive. Screens of wood cover the glass of the sides and top when the bees are not under observation. (Original.)

the dimensions of a large-sized rat, and the action of its legs and mandibles may be followed with great precision.

For the sake of later identification many of the bees are marked by painting different colors on their backs, and some are numbered. Such distinctive marks make it possible to follow the actions of an individual bee from day to day.

The observations here recorded were made during the summer of 1911 at the apiary of the Bureau of Entomology.

REMOVAL OF THE WAX SCALES.

The determination of the exact method by which the wax scales are removed either comes as the result of prolonged and patient watching or is the product of good fortune. Long before the observer is able to decide upon all of the details of the process he becomes convinced that usually the scales are removed by the bee which secretes them and by this bee are masticated and added to the comb. The workers never assist each other in the process of removal, although, as will be mentioned later, free scales may, in some cases, be handled by other workers.

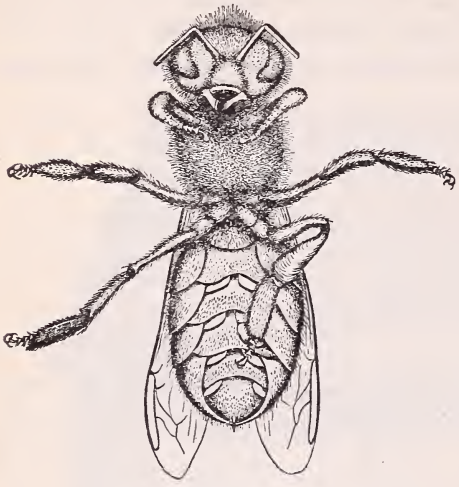

FIG. 3.—Ventral view of a worker bee in the act of removing a wax scale. The two middle legs and the right hind leg are used for support, while the left hind leg removes the scale. (Original.)

As a rule, the scales are removed while the bee is standing on the comb or its support, and the wax thus obtained is applied to the comb near the place where it is removed. Since the whole process of removal takes place beneath the worker's body it can be observed most satisfactorily when the bee is seen from the side or when it is building comb against a glass plate.

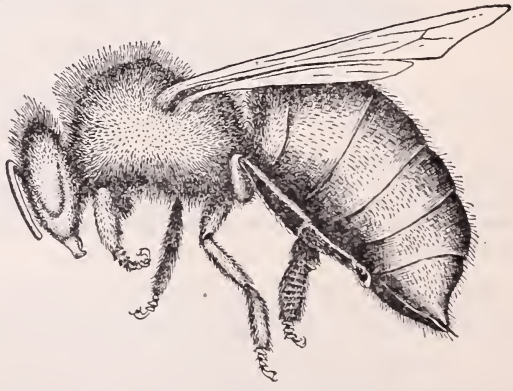

FIG. 4.—Side view of a worker in the same posture as that shown in figure 3. (Original.)

The posture of a bee in the act of removing a scale is rather characteristic and is at once recognized by one familiar with it. Immediately before the scale is to be removed the bee may be busily engaged upon the surface of the comb, plying with its mandibles the wax of the scale last extracted or reshaping and polishing wax already deposited, its whole body somewhat agitated, moving

backward and forward or from side to side as it adapts its position to the work in hand. Suddenly its body becomes very quiet. The forelegs and mandibles are raised from the comb, and the head is held with the face inclined toward the comb. The hind leg of one side is now raised, and its flattened first tarsal segment or planta is slipped along the ventral surface of the extended abdomen and comes in contact with the protruding wax scales of the corresponding side (figs. 3 and 4). The weight of the bee is now supported upon three legs; upon the middle leg of the side from which the scale is to be removed and upon the middle and hind legs of the other side. The first tarsal segment of the leg which is to remove the scale is now pressed firmly against the abdomen, and the edge of a protruding scale becomes engaged with it. Steady, continuous pressure is now exerted both against the abdomen and toward the rear, with the result that the scale is drawn out of its pocket but remains attached to the leg which removed it. The hind leg bearing the scale is now quickly flexed toward the thorax and head, thus carrying the scale forward under the body of the bee and placing it in a position where it may be readily grasped by the forelegs or the mandibles (figs. 5 and 6). Sometimes the scale is apparently removed from the hind leg by the mandibles alone, but usually the forelegs aid in this process and also manipulate the scale while

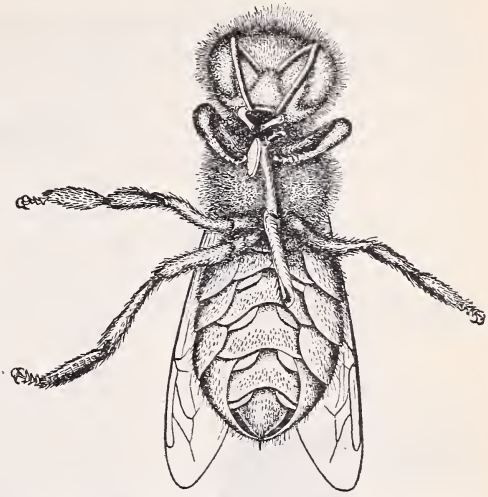

FIG. 5.—Ventral view of a worker bee showing the position of the wax scale just before it is grasped by the forelegs and mandibles. The scale is still adhering to the spines of the pollen combs. The bee is supported upon the two middle legs and upon the hind leg which is not removing the scale. (Original.)

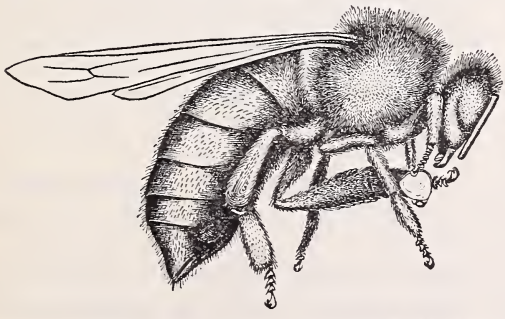

FIG. 6.—Side view of a worker bee in the same posture as that shown in figure 5. (Original.)

the mandibles are masticating it. After the scale has been thoroughly masticated the wax is applied to the comb.

THE SCALE-REMOVING ORGAN.

A point of particular interest in the process of wax scale removal is that which deals with the manner in which the scale is grasped by the hind leg which removes it. As is well known, each hind leg of the worker bee bears a pincerslike structure—the so-called wax shears—located at the juncture of the tibia and the flattened first tarsal segment or planta (fig. 7). According to the statements of numerous writers, the wax scales are grasped between the edges of the supposed pincers formed by the pecten above and the auricle below, and are either snipped off or are held by the jaws of the pincers and thus drawn from the pockets. Cowan's[1] account may be given as typical of others which are current in the literature of apiculture and of zoology.

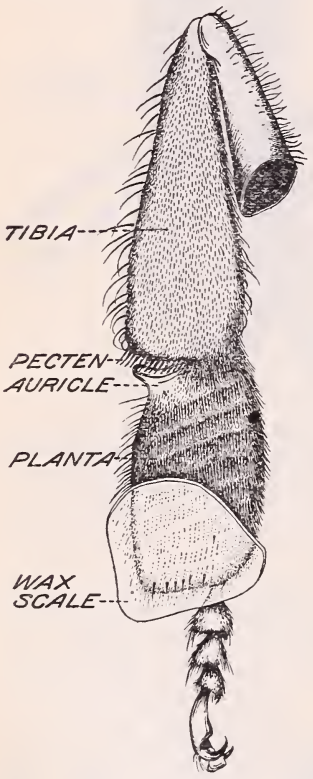

FIG. 7.—Inner surface of the left hind leg of a worker bee, showing the position of a wax scale immediately after it has been removed from the wax pocket. The scale has been pierced by seven of the spines of the pollen combs of the first tarsal segment or planta. The jaws of the so-called wax shears or pincers are formed by the pecten spines above and the surface of the auricle below. (Original.)

> The articulation of the tibia and planta being at the anterior angle, and the absence of the spur on the tibia (which only the honey bee does not possess) give the pecten a freedom of action it would not otherwise have and enable it to be used together with the auricle on the planta, which is quite smooth, as a true pair of pincers, and as an instrument for laying hold of the thin flakes of wax, and for bringing them forward to be transferred by the other legs to the jaws for manipulation.

As a matter of fact, the wax shears have nothing whatever to do with the removal of the wax scales. They perform an entirely different function, being concerned with the gathering of pollen in a manner to be described in a future paper.

In coming to the above conclusions the writer was first convinced that the so-called wax shears are not used in removing scales by noting that the position of the tibio-tarsal joint at the time of scale

[1] Cowan, T. W., "The Honey Bee," 2d ed., London, 1904.

removal is such as to make it impossible for the pincerslike crevice to grasp the scale. Moreover, the open jaws of the shears point laterally and away from the scales rather than toward them, nor, indeed, is it possible for the shears to grasp even the projecting edges of any of the ventral or lateral body plates and thus steady or guide the leg as it seeks contact with the scales.

The transverse rows of spines upon the planta, called pollen combs, and not the wax shears are instrumental in the removal of scales. Snodgrass (1910), in discussing the anatomy of the hind leg and its functions, states that the wax is "poked out of" the "pockets by means of the spines on the feet"—"with the ordinary hairs or spines of the tibiæ or tarsi," and the same general conclusions were reached independently by the writer, but with this exception; only the spines of the first tarsal segment (planta) function in this manner, and usually only certain large spines in the rows at the distal end of this segment.

It is exceedingly difficult to capture a bee at the very moment at which the scale is being drawn from its pocket and before it has been carried to the mouth, and even if this is accomplished the captive is very likely to drop the scale from the hind leg in its struggles to escape. If, however, one is successful, the scale-removing leg will show the little wax scale adhering to the distal end of the inner surface of the first tarsal segment, being pierced in several places by the strong spines which project from the lower rows of the pollen combs. (See fig. 7.)

It can also be shown experimentally that this method of removing the wax scales is entirely possible, for if the hind tarsus of a bee is mounted upon a small stick and is gently rubbed along the ventral side of a fully extended dead bee's abdomen, holding it in such a position that the pollen combs brush over the projecting edges of the scales, one of the scales will probably be removed and will be seen adhering to the spines in the manner above described.

In any hive where comb is being constructed rapidly many free scales will be found upon the bottom board and upon the lower bars of the frames. If these scales are examined microscopically some will be found without marks upon them, having evidently been loosened from their pockets accidentally during the movements of the workers over the comb and around the hive. Others will show certain marks and scratches upon them, indicating that they were voluntarily removed from the pockets, and in some cases they may bear the marks of the mandibles, showing that they were dropped during the process of mastication. Most of the scales which are marked at all are indented with several small punctures showing the places where the spines of the pollen combs have pierced them. These scars are exactly similar in appearance to those on the scale

shown in figure 7. Such free scales are not marked as they would be had they been extracted by such a structure as the so-called wax shears.

So far as can be determined there does not appear to be any regular order for the removal of scales. One may be taken from the left side and then one from the right, or the bee may remove two or three from one side in succession. An attempt to remove a scale is by no means always successful, the worker often trying first one side and then the other, pressing the pollen combs against the more anterior scales and running them down to the most posterior, until at last a scale is impaled upon the spines or the bee discontinues its efforts.

FURTHER MANIPULATION AND THE MASTICATION OF SCALES.

When a scale has become attached to the spines it is transferred to the mouth with great rapidity, so swiftly, in fact, that the eye can scarcely follow the action. This is not surprising, for it is necessary only to flex the leg toward the head to bring the scale in close contact with the forelegs and mandibles. The leg is rotated through the arc of a circle, downward, forward, and upward, while at the same time the head is slightly turned under to receive the scale. The process of mastication is more prolonged. It is usually supposed that the pure wax of the scale differs in chemical composition from the wax of the comb, this change being accomplished during mastication, by which process the wax is mixed with saliva, becomes translucent rather than transparent, changes somewhat in color, and becomes more pliable.

The behavior of a bee upon receiving a wax scale at its mouth is subject to considerable variation. On some occasions the scales are apparently manipulated by the mandibles alone, while at other times the forelegs are brought into requisition and assist the mandibles. When a scale is thin and small and has been firmly grasped by the mandibles little assistance is needed from the legs. But if a scale of medium or extra thickness is presented, or if the mandibles do not hold it securely and it is in danger of falling from the mouth, the two forelegs are used to great advantage in readjusting the scale and in so holding it that the mandibles may be applied to it most advantageously. If a scale is small and thin, it may be masticated entirely before any wax is applied to the comb; but if of considerable size a portion only may be prepared, this deposited upon the comb, and then the remainder treated in a similar manner.

As a rule the wax which is deposited upon the comb by the producing bee is first subjected to the action of the mandibles and mixed with saliva. Such, however, is not always the case, for some bees appear to be "careless" and will mingle small unchewed portions of scales with the masticated wax. Indeed, it is not uncom-

mon to find nearly perfect scales mixed with the wax of a newly made comb. The masticated wax itself is spongy and flaky when it is deposited by the producing bee and will later be reworked, thereby gaining greatly in compactness and smoothness.

The entire process of the removal of one scale, its mastication, and the application of the wax to the comb is completed in about four minutes, only a very small portion of this interval being consumed in the work of extracting the scale from its pocket and passing it to the mouth, except in cases in which scales appear to be removed with difficulty.

FREE SCALES.

When wax scales are voluntarily removed they are taken off by the bee which secretes them and in the manner above described. Many, however, are accidentally detached, being loosened from their pockets by movements of the abdomen, incidental cleansing movements of the legs, or by contact with objects both within and without the hive. Such scales, and also those which are dropped in the course of transference from the wax pocket to the mouth, may or may not be recovered later and added to the comb. Since old wax is used over and over again in the rebuilding of comb, it is but natural to expect that scattered scales would likewise be utilized by the colony and not be allowed to go to waste, and it is probably true that such is usually the case. Yet there appears to be no concerted action among the workers to salvage such particles of wax, no class of comb workers whose duty it is to pick such material from the bottom board of the hive and carry it to the comb. Scales which drop are likely to remain for a long time, and some may even be carried out through the entrance with waste material. If, however, scales accidentally dislodged or voluntarily removed fall on the comb among the comb workers they are often noticed by them, picked up, masticated, and built into the comb. If a scale slips from the pollen combs or is fumbled by the bee before being grasped by the mandibles, it is seldom recovered by the worker to which it belongs unless it falls very near her or she stumbles upon it accidentally.

PARTIAL REMOVAL OF SCALES.

Although a bee endeavors to remove an entire wax scale at one operation, the attempt is not always successful. A scale that has become very thick is difficult of removal, particularly so if the outer edge is broken or beveled. When the bee applies its pollen combs to such a scale the spines may fail to get a hold upon the wax, or they may not become sufficiently well fixed in it to make possible the removal of the entire scale. Instead of this, shreds and small pieces of wax are torn off and remain sticking to the bristles of the pollen

combs. These may be entirely disregarded by the bee, or they may be cleaned off by scraping the combs together, the shreds of wax dropping to the bottom of the hive. More usually, however, if a worker is actively engaged in the task of adding to the comb these bits of wax will be carried forward to the mouth, masticated, and applied.

In one case which came under observation a worker had removed all of its wax scales except a very large, thick one which was evidently sticking tightly in its pocket. Repeated efforts were made by the bee to accomplish the extraction of this scale, but with only partial success, since the main portion of the scale remained in the pocket. But as the result of its efforts the bee succeeded in beveling off the entire projecting edge of the scale, rasping it off bit by bit and carrying the small pieces forward to the mouth, masticating them, and dispositing the wax upon the comb.

PRODUCERS AND BUILDERS.

The presence of well-developed scales protruding from the pockets of a worker does not necessarily indicate that this individual will shortly add this wax to the comb, even though the colony may at the time be producing comb at a rapid rate. Such a bee may be working upon the comb as a molder of wax rather than as a producer. One who is intent upon a study of the process of scale removal will often be disappointed after following for a time the movements of a worker that is evidently manipulating wax and which shows the protruding edges of scales beneath its abdomen, for the wax with which it is working is being picked up, little by little, from the comb and comes not from its own body. This reworking of wax is one of the most characteristic features of comb construction, for it goes on continually while new comb is being produced, and it is, of course, a necessary process in the reconstruction of old comb.

The claim has been made by several investigators and writers that the bees which sculpture the wax are not at the same time concerned with its secretion and deposition—that there are producing bees and building bees. In a sense this is true, but not entirely so. Without doubt many active comb workers are, at the time, nonproductive, for the wax glands of many are not functionally active. The results of Dreyling would indicate that the old bees, at least, might be considered as falling in this class, and the direct observations of the writer lead to the conclusion that old bees devoid of wax scales perform a considerable share of the labor of reworking newly deposited wax and of shaping and polishing the cells of the comb.

However, as noted above, bees with well-developed wax scales often busy themselves with wax working rather than with production. Moreover, a bee that is removing its scales may discontinue

this work and give its attention to the molding of wax laid down by others. This may occur immediately after a worker has removed the last of its scales, or the bee may turn to sculpturing while several scales yet remain in the pockets. It is thus evident that the producing bee may also be a worker of wax produced by others and that nonproductive bees do not monopolize the work of sculpturing and polishing the comb.

SUMMARY.

As is well known, the wax produced by the worker bee occurs in the form of scales, eight in number, which appear upon the surfaces of the eight wax plates. These wax plates are located upon the last four visible ventral plates of a worker bee's abdomen. The wax is secreted by glands which lie upon the inner surface of each wax plate. The liquid wax exudes through pores which perforate the wax plates, and it hardens to form the scales as it comes in contact with the air.

Unless accidentally dislodged the wax scales are always removed and manipulated by the bee which secretes them.

In the process of removal the scale is not grasped by the so-called wax shears, but it is pierced by a few of the stiff spines on the distal end of the first tarsal segment of the hind leg and is then drawn from its pocket and remains adhering to these spines until removed for mastication.

By flexing the hind leg the scale is brought forward beneath the bee's body and into proximity with the mouth. In the process of mastication the forelegs usually aid the mandibles by holding the scale in an advantageous position.

No definite sequence is observed by the bee in the order in which it removes its scales.

As a rule entire scales are removed at one operation, although it sometimes happens that a thin scale is broken in extracting it from its pocket or an extremely thick one is gradually beveled off by the continued rasping of the pollen combs.

Scales which are removed accidentally or which are dropped during manipulation may be recovered later and built into the comb, but the recovery of free scales is usually not accomplished by the bee which secreted them.

Bees which are producing wax may also rework the masticated wax laid down by others. Producing bees may turn to the work of building and sculpturing the comb either before all their scales are removed or immediately after this has been accomplished.

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